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Infant Japanese macaque food selection

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ABSTRACT

Dietary differences exist between infant and adult female non-human primates. These differences are considered to be related to the low ability of infants to bite, handle, and obtain food items. This study aimed to provide a comprehensive examination of how the physical properties of food items (fracture toughness, size, processing, and height) influence food selection by infant primates. In this study, 4 mother–infant Japanese macaque (*Macaca fuscata*) pairs were investigated in a snow-covered area during winter. The feeding behavior of both mothers and infants was recorded. The size, need for processing, and height of food items were recorded by direct observation, while the fracture toughness of food items (evaluating the required bite force by incisors) was measured using a rheometer. On average, infants spent 14% less time feeding than their mothers, and there were dietary differences between mothers and infants. Compared to their mothers, infants fed relatively more frequently on food items that were small, at a low position, or that could be consumed without processing. In addition, infants spent less time feeding on food items that were tougher than 2000 J/m^2. Thus, infants fed relatively more frequently on food items that are easy to obtain. This food selection by infants reduced the costs of feeding and allowed them to avoid falling from high trees.

Key words: food characteristics, food access and processing, bite force, relative feeding index, age differences

INTRODUCTION

Many studies of non-human primates indicate that food selection by mothers affects food selection by their infants [for review, see Rapaport & Brown, 2008]. When infants start to eat solid foods, they copy the food selected by their mothers [Hikami et al., 1990; Jaeggi et al., 2010]. Yet, some studies have reported the presence of dietary differences between infants and adult females [Nakayama et al., 1999; Tarnaud, 2004], which are attributed to the physical [Altmann, 1980; Gunst et al., 2008; Gunst et al., 2010] and physiological [Nakayama et al., 1999] differences between the 2 age classes. Altmann [1980] observed that “weaning foods” are foods that are easily obtained and are eaten by infants during the transition from dependence on milk to full nutritional independence. Therefore, the physical properties of food items may partly influence food selection by infants during the period of weaning.

First, previous studies have shown that the toughness of food items influences food selection by infants. In long-tailed macaques (*Macaca fascicularis*), infants avoid eating fruits with hard rinds [van Schaik & van Noordwijk, 1986]. A craniofacial biomechanical study in rhesus macaques (*Macaca mulatta*) showed that the mean incisor bite force of juveniles is half that of adults [Dechow & Carlson, 2005]. Thus, the bite force in infants is considered to be much weaker than that of adults. In recent decades, several studies have used quantitative methods to examine how the toughness of food items influences food selection in primates [Hill & Lucas, 1996; Kinzey & Norconk, 1990]. These studies revealed a relationship between the ability to process food items and morphological features via interspecific and intraspecific comparisons [McGraw et al., 2011; Norconk & Veres, 2011; Vogel et al., 2008; Vogel et al., 2014, Wright et al., 2008]. However, previous studies have not quantified the effect of food toughness on food selection by infants.

Second, the size of food items may affect food selection by infants. Infant long-tailed macaques eat relatively smaller fruits than adults [van Schaik & van Noordwijk, 1986]. Since bite size can be a body-mass dependent trait of the masticatory apparatus, large-bodied animals generally feed on large food items more efficiently than small-bodied animals. On the other hand, small-bodied animals need to bite large food items many times [Nakagawa, 2008; Shipley et al., 1994; Wrangham et al., 1993].

Third, food items that need processing skill may affect food selection by infants. Several studies suggest that infants are less efficient foragers than juveniles and adults [Gunst et al., 2008; Gunst et al., 2010; Rhine & Westlund, 1978; Stone, 2006]. For example, compared to juveniles and sub-adults, western lowland gorilla (*Gorilla gorilla*) infants tend to feed on food parts that are easier to obtain and that require no processing, because they lack the processing skills and physical strength (e.g., arm strength) necessary to access hard-to-process food items [Nowell & Fletcher, 2008].

Fourth, another factor that might influence food selection by infants is the height at which food items are located. Before infants achieve full motor competence, climbing and moving arboreally might increase the probability of fatal falls [Chalmers, 1972; Dunbar & Badam, 1998; Karssemeijer et al., 1990; Sussman, 1977]. In addition, compared to other age classes (particularly juveniles), rhesus macaque infants spend more time in low and stable positions [Wells & Turnquist, 2001].

Thus, food selection by infants is considered to be affected by the physical properties of food items, including toughness, size, processing, and height. However, previous studies only focused on a limited set of food items [Altmann, 1980; Gunst et al., 2008; Gunst et al., 2010; Nowell & Fletcher, 2008; Rhine & Westlund, 1978] and on certain categories of food parts (e.g., fruits, leaves, and bark) [Nakayama et al., 1999; Tarnaud, 2004]. Few studies have considered all food items when examining the influence of the physical properties of food on dietary differences between infant and adult primates.

In temperate regions, it is important to survive in winter when the climate is harsh (i.e., cold and snow) and food availability is low [Nakagawa, 1997]. The Japanese macaque is the best-studied temperate primate, with its seasonal reproductive and foraging patterns being well-documented [Nakagawa et al., 2010]. Thus, this species presents an ideal model for studying age-related differences on revealing the feature of food selection by infants. Infant Japanese macaques (*Macaca fuscata*) are born in spring and need to eat solid foods before the onset of winter to meet their nutritional requirements, because the daily rate of milk transfer from mothers decreases by 50% at around 6 months of age [Tanaka, 1992]. Indeed, infant macaques start to increase solid food intake at 5–6 months of age [Iwamoto, 1982]. In snow-covered areas with cool-temperate deciduous forests, macaques are limited to bark and dormant buds as their main food items in winter [Suzuki, 1965]. Dietary differences between infant and adult female Japanese macaques have been previously reported. For instance, infants primarily feed on buds in winter, whereas adult females mainly feed on bark [Nakayama et al., 1999].

This study aimed to provide a comprehensive examination of the physical properties that influence food selection by infant Japanese macaques. I hypothesize that, compared to their mothers, infants feed more frequently on food items that are easily obtainable, because infant have a lower ability to bite, handle, and acquire food items. Specifically, I hypothesize that, in comparison to their mothers, Japanese macaque infants feed relatively more frequently on food items that (1) are softer; (2) can be eaten in 1 bite; (3) do not need processing; and (4) are located at a lower position in trees. In particular, it may be easy to validate the effect of the height of food items in snow covered areas, because macaques tend to be limited to using food items on trees (as ground vegetation is covered in snow) [Suzuki, 1965]. In addition, a large number of studies have been conducted on the morphological development of Japanese macaques, in terms of teeth and locomotor apparatus [Hamada, 1982; Hamada, 1983; Ishida, 1972; Iwamoto, 1977; Iwamoto et al., 1984; Iwamoto, 1987]. Thus, the feeding pattern observed in the current study is discussed in relation to the morphological development of this species, to validate my hypotheses.

METHODS

This study complied with the research guidelines of the Primate Research Institute of Kyoto University, Japan, and adhered to Japanese legal requirements. I also adhered to the Principles for the Ethical Treatment of Nonhuman Primates delineated by the American Society of Primatologists.

Study area and subjects

The study was conducted in the southwestern part of the Shimokita Peninsula (41°30′N, 141°00′E) from December 27, 2008 to March 29, 2009. The forest located at an altitude higher than 400 m above sea level (a.s.l.) is dominated by *Fagus crenata* and *Sasa* species on the forest floor. In comparison, the forest located at an altitude below 400 m a.s.l. is a mosaic dominated by *Thujopsis dolabrata* and *Quercus crispula*. Approximately one-quarter of the forest is covered in plantations or secondary forests of *Cryptomeria japonica*, *Pinus densiflora*, *Larix kaempferi*, and *Abies sachalinensis* [Kanuma et al., 2000].

The daily mean temperatures during the study period were 1.1 ± 2.6 °C (mean ± SD, range = -4.5–10.9 °C), and the daily mean minimum temperatures were -2.2 ± 2.2 °C (range = -7.3–6.7 °C) (Japanese Meteorological Agency; http://www.jma.go.jp/jma/index.html; accessed 2013-10-31). The study area was covered in snow during this period; however, snow was sometimes absent in certain places (e.g., roads).

The study group was the A87 troop of Japanese macaques, comprising 51 individuals, including 13 adult females (estimated as being either over 7 years of age or parous) and 7 infants (less than 1 year of age). Four mother–infant pairs (Pairs ID1, ID2, ID3, and ID4) were investigated in this study. The ages of the infants ranged between 7 and 10 months during the study period. The focal infants consisted of 2 males and 2 females.

The focal mother–infant pairs were investigated by the focal animal sampling method [Altmann, 1974]. Either a mother or her infant was observed as the focal animal. Then, each animal was observed for 10 hours every 3 weeks. The total observation time for each animal was 40 hours during the study period. Each animal was continuously observed for 1 hour at a time. I changed focal animals each hour, unless no other subject individuals were within view of the observer.

The focal animal's activities (feeding, grooming, resting, traveling, and other), maternal carriage, and nipple contact were recorded by instantaneous sampling

[Altmann, 1974] at 3-min intervals. In this study, I present data for infants relating to the time spent in contact with the mother's nipple and carriage by the mother. The definition of "feeding" included not only taking food items into the mouth, but also processing (e.g., removal of a husk or digging an item out of the ground), and searching for (e.g., raking fallen leaves) food items by hand. When feeding was observed, I recorded the food item species, the food parts, the size of the food items, the need for processing, and the height at which feeding activity occurred. The food item parts were categorized as bark, dormant buds, leaves, seeds (including acorns and pinecones), roots (including rhizomes), twigs, and other. The size of food items was classified into 2 categories: (1) small: a food item entering an infant's mouth in 1 bite (less than approximately 1 cm in width), and (2) large: 2 or more bites required. The processing of food items was divided into 2 categories: (1) no processing required before a food item was taken into the mouth, and (2) processing required before a food item was taken into the mouth. The average height of food items was classified into 5 categories: (1) 0 m (i.e., on the ground), (2) 0–2 m, (3) 2–5 m, (4) 5–10 m, and (5) more than 10 m.

Measurement of fracture toughness

Previous studies have found that forces at the molars are 2–2.5 times greater than those at the incisors [Dechow & Carlson, 2005]. Therefore, in this study, I limited the measurement of fracture toughness to food items where macaques were observed to use their incisors to make the initial bites. I measured the fracture toughness of the 32 food items that macaques fed on for more than 1.0% of total feeding time. I could not collect or measure 3 food items (bark of *Helwingia japonica*, acorns of *Q. crispula*, *Trametes* spp.) among them. The bite force for bark, dormant buds, leaves, roots, and twigs was measured using a rheometer (COMPAC100II; SUN Scientific Co., Ltd. ™, Setagaya-ku, Tokyo, Japan). The rheometer measures a series of loads when a single blade cuts a food item. The load data were transferred to a computer using an analogue-digital converter (ADA16-32/2(CB)F, CONTEC Co., Ltd.®, Nishiyodogawa-ku, Osaka, Japan). The load was measured every millisecond during the cutting process. The total workload was calculated as the integral of the series of loads. Before taking rheometer measurements, the cross-sectional area was measured using a digital caliper (CD-15PSX; Mitutoyo Corporation ®, Kawasaki-shi, Kanagawa, Japan). The fracture toughness (J/m^2) was determined using the total workload and cross-sectional area. The fracture toughness of each food item was measured more than 7 times, and the average of these measurements was used for analyses. The mechanical tests of food items were performed within 6 hours of collection. The fracture toughness was classified into 6 categories: (1) less than 500 J/m^2, (2) 500–1000 J/m^2, (3) 1000–1500 J/m^2, (4) 1500–2000 J/m^2, (5) 2000–2500 J/m^2, and (6) more than 2500 J/m^2.

Food items for the measurement of fracture toughness were collected from February 5 to 29, 2012. Bark was collected from the same twigs from which the macaques ate bark. The bark was peeled off from the twig with the cambium layer for the analysis. When I was unable to collect the twigs that the macaques fed on, I collected the bark of similar twigs from the same tree. Dormant buds were measured from the boundary between the bud and the twig. Leaves were measured from the middle of the lamina without the midrib, because macaques sometimes did not feed on the midrib. Roots were measured from the boundary between the leaves and roots.

Rhizomes were measured at the mid-point between joints. Young twigs were collected from the same tree from which a macaque fed on twigs. Macaques fed on the top part of young twigs. I measured the position of the length 1 cm from the top of young twigs, where macaques often fed. I could not always identify the species name of ferns. The fracture toughness of ferns was based on the average fracture toughness of *Polystichum tripteron*, on which macaques often fed.

Relative feeding index

For each mother–infant pair, the difference in time spent feeding on each food item by the mother and its infant was calculated using the following formula [Ichihara, 1990]:

$$\textbf{Relative feeding index of food item X} = \frac{(\mathbf{P_1} - \mathbf{P_2}) - \mathbf{0}}{\sqrt{\mathbf{P}(\mathbf{1}-\mathbf{P})\left(\frac{\mathbf{1}}{\boldsymbol{n_1}} + \frac{\mathbf{1}}{\boldsymbol{n_2}}\right)}}$$

n_1 = Mother's total number of feeding sample points

n_2 = Infant's total number of feeding sample points

$n_{1\ \text{food item X}}$ = Mother's number of sample points feeding on food item X

$n_{2\ \text{food item X}}$ = Infant's number of sample points feeding on food item X

$$P_1 = \frac{n_{1\ \text{food item X}}}{n_1},\ P_2 = \frac{n_{2\ \text{food item X}}}{n_2},\ P = \frac{n_{1\ \text{food item X}} + n_{2\ \text{food item X}}}{n_1 + n_2}$$

A negative number indicates that an infant fed more on a given food item than its mother, whereas a positive number indicates the opposite. To remove the effect of food items on which macaques fed less, the index of the food item where $n_{1\ \text{food item X}} + n_{2\ \text{food item X}}$ was greater than 10 sample points was subject to statistical analysis for each pair.

Statistical analysis

To examine the influence of physical properties on the dietary difference between mothers and infants, I used a generalized linear mixed model (GLMM), assuming a normal distribution, with the relative feeding indices as a dependent variable, and 3 physical properties (size, processing, and height) as independent variables for each food item. I set the mother–infant pair ID as a random effect. Before using the GLMM, I checked whether the data set for the relative feeding index had a normal distribution using a Kolmogorov–Smirnov test. In addition, I calculated the variance inflation factors (VIF) among 3 factors (size, processing, and height) to check for multicollinearity. Montgomery and Peck [2001] suggest that if the VIF is over 5, the regression coefficients are poorly estimated. The VIF among the 3 factors was low enough for the analyses. Moreover, I added fracture toughness as an independent variable in the GLMM analysis for the measured food items. The normal distribution of the relative feeding indices was checked by the same method presented previously. The VIF among the 4 factors (size, processing, height, and toughness) was low enough for the analyses.

All possible combinations of independent factors were examined, and model fitness was assessed by the Akaike Information Criterion (AIC) [Burnham & Anderson, 2002]. I examined only the models that had a ΔAIC (difference from the smallest AIC) of less than 2. To assess the relative likelihood of these models, I calculated the Akaike weight as exp(-0.5 × ΔAIC score for that model)/sum of exp(-0.5 × ΔAIC score) for all of the models [Burnham & Anderson, 2002]. I presented the coefficient from the maximum-likelihood estimation in the best-fit model with the smallest AIC. In the physical properties selected for the best-fit model, the statistical difference was determined by the Mann-Whitney test or the Kruskal-Wallis test. For each pair, the dietary differences between the infant and its mother were analyzed using the χ^2 test. Differences with a *P* value of less than or equal to 0.05 with a two-tailed test were considered significant. I used the software program R 3.0.3 (The R Foundation for Statistical Computing; http://www.r-project.org/) for all statistical analyses.

RESULTS

General description of feeding behavior

During the study period, mothers and infants spent 44.8 ± 6.3% ($N = 4$, range = 40–54%) and 37.9 ± 4.8% ($N = 4$, range = 32–44%) of time feeding on solid food items in total observation time, respectively. The infant/mother ratio for time spent feeding was 0.86 ± 0.17 ($N = 4$; range = 0.72–1.09). The time spent in contact with the mother's nipple was 21.3 ± 5.6% ($N = 4$, range = 17–29%) and the time spent carriage by the mother was 0.41 ± 0.24% ($N = 4$, range = 0.25–0.75%).

For all 4 mother–infant pairs, a dietary difference was present between the mother and its infant in terms of dietary composition of food items that were used in the calculation of relative feeding index (Table I; χ^2 test: pair ID1, $\chi^2 = 193.76$, $P < 0.01$, d.f. = 10; pair ID2, $\chi^2 = 93.76$, $P < 0.01$, d.f. = 12; pair ID3, $\chi^2 = 112.88$, $P < 0.01$, d.f. =11; pair ID4, $\chi^2 = 133.68$, $P < 0.01$, d.f. = 15). Table I shows the average time spent feeding on each food item by mothers and infants. Among the top 5 food items in terms of the time spent feeding, both mothers and infants contained leaves of Poaceae spp. and acorns of *Q. crispula*. The remaining 3 top food items differed between mothers and infants; infants contained buds of *Sasa kurilensis*, buds of *Zanthoxylum piperitum*, and leaves of *Carex* spp., whereas mothers contained seeds of *P. densiflora*, bark of *Actinidia arguta*, and roots of *Trifolium repens*.

Relationship between the relative feeding index and 3 physical properties of food items

I examined the relationship between the relative feeding index and 3 physical properties of each food item (size, processing, and height). Fifty-two relative feeding indices ($N_{\text{pair ID1}} = 11$; $N_{\text{pair ID2}} = 13$; $N_{\text{pair ID3}} = 12$; $N_{\text{pair ID4}} = 16$), including 23 different food items, were analyzed (Table I). For mothers, the percentage of time spent feeding on the food items used in this analysis to total feeding time was 79.0 ± 2.8% ($N = 4$; range = 75–81%), whereas that for infants was 72.3 ± 6.0% ($N = 4$; range = 69–81%). The data set for the relative feeding index did not differ significantly from a normal distribution (Kolmogorov–Smirnov test, $D = 0.13$, $N = 52$, $P > 0.1$). All 3 properties influenced the difference in time spent feeding by mothers and infants in the best-fit model. Compared to the mothers, infants fed more on food items that could be consumed in 1 bite, that required no processing, and that were located at a lower position (Tables IIa, IIIa and Fig. 1). Food item size and height were selected by the second fit model with a ΔAIC of less than 2, and processing was not selected (Table IIa).

The size of the food item significantly affected the difference between mothers and infants (Tables IIIa). Food items that infants could eat with 1 bite mainly included buds (Fig. 1a).

Although the need to process food items led to differences in food selection between infants and mothers, there was no significant difference between food items that did and did not require processing in the relative feeding indices (Tables IIa and IIIa). Food items that required processing contained roots and seeds, and the average relative feeding indices of 2 food items (*Q. crispula* acorns and *P. lobata* seeds) had negative numbers (Fig. 1b). For instance, the average relative feeding index of *Q. crispula* acorns (Table I; Food item No. 2) was -1.04 ± 2.31 (N = 4; range = -4.2–1.0). Infants did not tend to spend less time feeding on *Q. crispula* acorns, which required the cracking of the shells. In addition, the infants spent more time feeding on *P. lobata* seeds (No. 11), which required the shelling of pods (χ^2 test: pair ID1, χ^2 = 21.58, P < 0.01, d.f. = 1).

Finally, the height of the food item significantly affected the difference between mothers and infants (Tables IIIa). All average relative feeding indices of food items that were located at a height of more than 5 m were positive numbers (Fig. 1c), except for *A. arguta* buds (No. 9). Infants spent more time feeding on *A. arguta* buds (χ^2 test: pair ID4, χ^2 = 11.75, P < 0.01, d.f. =1). For the 23 food items (Table I), mothers and infants spent 24.9 ± 4.1% (N = 4; range = 21–31%) and 7.9 ± 3.3% (N = 4; range = 4.8–12%) time, respectively, feeding on food items that were located at a height of more than 5 m in the tree in total feeding time. For all 4 mother–infant pairs, infants spent significantly less time feeding on food items that were located at a height of more than 5 m than their mothers (χ^2 test: pair ID1, χ^2 = 34.59, P < 0.01, d.f. = 1; pair ID2, χ^2 = 26.83, P < 0.01, d.f. = 1; pair ID3, χ^2 = 19.46, P < 0.01, d.f. = 1; pair ID4, χ^2 = 21.98, P < 0.01, d.f. = 1).

Relationship between the relative feeding index and 4 physical properties of

food items

To clarify the influence of fracture toughness on dietary differences between mothers and infants, I examined the relationship between the relative feeding index and 4 physical properties (fracture toughness, size, processing, and height) of the food items. Thirty-nine relative feeding indices were analyzed ($N_{\text{pair ID1}}$ = 7; $N_{\text{pair ID2}}$ = 10; $N_{\text{pair ID3}}$ = 9; $N_{\text{pair ID4}}$ = 13), including 19 different food items for which macaques were observed to use their incisors in taking the initial bites (Table I). For mothers, the percentage of time spent feeding on the food items used in this analysis to total feeding time was 57.5 ± 8.1% (N = 4; range = 46–65%), whereas that for infants was 50.1 ± 13.1% (N = 4; range = 31–60%). This dataset contained only 1 of 4 food items that required processing. The dataset relating to the relative feeding index did not differ significantly from a normal distribution (Kolmogorov–Smirnov test, D = 0.15, N = 39, P > 0.1). In the best-fit model (Tables IIb and IIIb), size, height, and processing affected the difference in the time spent feeding by mothers and infants, and each effect had the same tendency as the above analysis (Tables IIa and IIIa). Fracture toughness was not selected in the best-fit model (Table IIb). However, the second fit model with a ΔAIC of less than 2 contained fracture toughness.

Although fracture toughness did not cause a major difference in the selection of food between mothers and infants, all average relative feeding indices of the food items that were tougher than 2000 J/m^2 were positive numbers (Fig. 1d). Among the 32 food items for which fracture toughness was measured, all infants spent significantly less time feeding on food items that had a toughness of more than 2,000 J/m^2 (Fig. 2; χ^2 test: pair ID1, χ^2 = 5.37, P < 0.05, d.f. = 1; pair ID2, χ^2 = 30.87, P <

0.01, d.f. = 1; pair ID3, χ^2 = 35.01, *P* < 0.01, d.f. = 1; pair ID4, χ^2 = 34.34, *P* < 0.01, d.f. = 1). Food items that were tougher than 2000 J/m^2 included some bark, *Z. piperitum* twigs, *S. kurilensis* leaves, and *Miscanthus sinensis* roots.

DISCUSSION

The results of this investigation were almost concordant with my hypothesis. In summary, compared with their mothers, Japanese macaque infants fed relatively more on food items that are small, that require no processing, or that are located at a lower position. In addition, infants spent less time feeding on food items with a toughness greater than 2,000 J/m^2.

Feeding and suckling by infants

Throughout the study period, Japanese macaque infants still spent as much as 21.3% of their time suckling, and the average time spent feeding was 0.86 times that observed in mothers. This result is almost consistent with the findings of a previous study. In winter, Japanese macaque infants inhabiting a snow-covered areas, spent approximately 30% less time feeding than adult females [Nakayama et al., 1999]. Nakayama and others [1999] suggest that the estimated fuel reserves do not meet the cumulative energy deficit of infants and adult females during winter, and the energy deficit of infants might be met by consuming milk from their mothers. Thus, infants need to feed on solid food, in addition to spending more time suckling during winter.

Relationship between food fracture toughness and food selection by infants (Hypothesis 1)

Although infants did not feed relatively more frequently on food items that were softer, they spent less time feeding on food items that were tougher than 2000 J/m^2 compared to their mothers. These quantitative results are consistent with those of previous studies of long-tailed macaques that were conducted using qualitative methods [van Schaik & van Noordwijk, 1986]. The ability to process food is known to be linked with the morphology of different species or age–sex class [McGraw et al., 2011; Norconk & Veres, 2011; Vogel et al., 2008; Vogel et al., 2014; Wright et al., 2008]. Deciduous dentition is complete at around 7.5 months of age in Japanese macaques, and the age of eruption of the permanent teeth is around 18 months [Iwamoto et al., 1984; Iwamoto, 1987]. Therefore, the infants observed during the present study period had completed deciduous dentition, but did not have permanent teeth. According to a craniofacial biomechanical study [Dechow & Carlson, 2005], when juveniles reach complete deciduous dentition, but occlusion of the first permanent incisors has yet to occur, the mean forces of juvenile incisors are only half those of adults. Thus, differences in the fracture toughness ranges of food items selected by mothers and infants might be the result of differences in their morphological features.

Relationship between food size and food selection by infants (Hypothesis 2)

Infants fed relatively more frequently on food items that could be eaten in 1 bite compared to their mothers. Bite size (amount of food eaten with a single bite) constrains the feeding rate [Nakagawa, 2008, Shipley et al., 1994]. The bite size of large food items increases with body size. Consequently, mothers feed more on larger food items than their infants. In addition, small animals are considered to need more time to process large food items than large animals [Nakagawa, 2008; Wrangham et al., 1993]. For instance, the feeding rate on buds was greater than that on bark in 0 year olds and 1 year olds whereas there was no difference in the feeding rate of these 2 food parts by older Japanese macaque classes [Nakayama et al., 1999]. Infants may increase their feeding efficiency by selecting smaller food items.

Relationship between food processing and food selection by infants (Hypothesis 3)

Infants tended to feed relatively more frequently on food items requiring no processing than their mothers. However, processing was not selected by the second fit model, with no significant difference between food items that did and did not require processing in the relative feeding index.

Food items that require processing included roots, which that need to be dug out, and pinecones, the scales of which need to be peeled off. It might be difficult for infants to feed on food items that require high arm strength and/or bite force for processing. Juvenile chacma baboons (*Papio hamadryas ursinus*) are significantly less efficient foragers than adult baboons primarily for difficult-to-extract resources [Johnson & Bock, 2004]. In addition, adult Japanese macaques carry and wash grass roots, while juveniles have rarely been observed to dig roots [Nakamichi et al., 1998]. Nakamichi and others [1998] discussed the possibility that it may be difficult for juveniles to dig out roots. In brown capuchins (*Cebus apella*), infants do not have adult levels of proficiency at ripping bamboo stalks to extract larvae, with infants devoting more time than adults and juveniles to foraging on other food items (shoots, pith, and non-embedded insects) that are easy to obtain [Gunst et al., 2008]. It has been suggested that foraging efficiency and time allocation are linked to parallel changes in body size and dentition [Gunst et al., 2008]. The results of this study are generally consistent with these preceding studies.

Yet, the average relative feeding indices of 2 food items (*Q. crispula* acorns and *P. lobata* seeds) had negative numbers. For both mothers and infants, *Q. crispula* acorns (No. 2) were among the top 5 food items, and infants tended not to spend less time on this food item than their mothers. In addition, infants fed more frequently on *P. lobata* (No. 11) seeds, which required the pods to be shelled. Out of the food items available in winter, acorns and seeds have higher energy or protein content compared to other food items (e.g., bark, leaves, and buds) [Nakagawa, 1989; Nakagawa, 1997]. In particular, primate infants have a higher requirement for protein compared to adults [Oftedal et al., 1991]. If infants are able to access energy- or protein-rich food items that need processing, infants may feed at the same time as their mothers or may feed on these items more frequently than their mothers. However, to confirm these hypotheses, I must conduct a more detailed examination of on the processing of food items, and the relationship between the physical properties and nutritional content of food items.

Relationship between food height and food selection by infants (Hypothesis 4)

Infants fed relatively more frequently on food items that were located at low positions than their mothers. Since infants were only carried for 0.41% of the time, infants had to climb trees by themselves to feed on solid foods in winter. In addition, Japanese macaque infants over 4 months of age tend to decrease their proximity to their mothers when feeding [Ueno, 2005]. Infant rhesus macaques also use the ground and low or horizontal arboreal settings more than adults and juveniles [Wells & Turnquist, 2001]. Wells and Turnquist [2001] noted that ontogenetic changes in morphology are closely paralleled by changes in locomotor behavior.

In studies on the growth of the locomotor apparatus of Japanese macaques, the most notable ontogenetic changes in the musculoskeletal system occur during the first year of life. There is a shift from the newborn pattern of the propulsive mass of the hind limb in yearlings [Hamada, 1982; Hamada, 1983] and the locomotor apparatus acquires approximately the pattern of adults when monkeys are around 2 years of age [Ishida, 1972]. As infants grow up, their upper limb muscles develop for forward propulsion, including pulling up the body when climbing, in addition to improving the control of the movement of segments at the shoulder, elbow, and wrist joints. In contrast, the necessity for finger extension and flexion with power decreases [Hamada, 1982; Hamada, 1983; Ishida, 1972]. Thus, it may be more difficult for infants to move in trees because their locomotor apparatus is shifted toward quadrupedalism.

Compared to their mothers, infants fed more frequently on food items located less than 5 m above the ground. Infants may avoid the risk of falling from a high position by selecting the lower positions as feeding sites. However, compared to their mothers, infants fed more on *A. arguta* buds (No. 9), which are positioned more than 5 m high. *A. arguta* is a woody liana that twines around itself and forms a stable foothold. Thus, *A. arguta* may be more accessible to infants than other food items that are located at a height of over 5 m.

Incidentally, it has been reported that the time allocated to arboreal travelling was longer for juveniles than adults [Hanya, 2003; Watanuki & Nakayama, 1993].

Arboreal feeding is advantageous for juveniles when eating buds and fruits on terminal twigs, because increased body mass may restrict immediate access to terminal twig areas [Hanya, 2003; Watanuki & Nakayama, 1993]. However, the results of this study indicate that smaller body mass may not be an advantage for infants when moving to terminal twigs at heights of over 5 m. In rhesus macaques, juveniles (12–18 months of age) spent more time in the arboreal environment than adults and infants [Wells & Turnquist, 2001]. This difference in the behavior pattern of juveniles and adults may be explained by the inverse relationship between body size and joint mobility, because there is a rapid decline in passive joint mobility until an age of approximately 15 months [DeRousseau et al., 1983]. In addition, juveniles are able to move more freely than infants, which do not have fully developed locomotor apparatus [Dunbar & Badam, 1998]. In comparison with mothers and juveniles, infants probably spend more time feeding on food items at lower positions in the tree after decreasing maternal carriage.

The results of the current study were almost concordant with my hypothesis that infants feed more frequently on food items that are easily obtainable than their mothers, because of the lower ability of infants to bite, handle, and access food items. These preferences, which are associated with the physical abilities of infants, save the costs of time and energy required for feeding [Janson et al., 1993; Johnson & Bock, 2004], and help infants to avoid falling from high trees. During the weaning period, infants may acquire information about available foods or foraging skills from their mothers [Tarnaud & Yamagiwa, 2008], while they spend more time feeding on easily obtainable foods, termed “weaning foods.”

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TABLE I. Percentage of time spent feeding by infants and mothers, the relative feeding index, and the physical properties of food items. Percentage of time spent feeding on food items was averaged for 4 focal infants and 4 focal mothers. The food items were arranged according to the time that infants spent feeding on them. The relative feeding index of the food item was averaged among mother–infant pairs that were used in the calculation of the relative feeding index.

			Percentage of time spent feeding				Relative feeding index		Physical properties of the food item			
Food item No.	Food item species name	Food part	Infant	※	Mother	※		※※ (Pair ID name)	Size	Processing	Height	※※※ Toughness
1	Poaceae spp.	Leaf	23.1	1	24.7	1	0.43	4 (All)	2	1	1	2
2	*Quercus crispula*	Seed (Acorn)	12.0	2	9.1	3	-1.04	4 (All)	2	2	1	-
3	*Sasa kurilensis*	Bud	8.2	3	1.9		-3.69	4 (All)	1	1	1	-
4	*Zanthoxylum piperitum*	Bud	8.2	3	2.3		-3.47	4 (All)	1	1	2	2
5	*Carex* spp.	Leaf	5.1	5	3.6		-1.05	3 (ID1, 3, 4)	2	1	1	3
6	*Fraxinus lanuginosa*	Bud	2.8		1.9		-0.97	4 (All)	1	1	3	3
7	*Viburnum dilatatum*	Bud	2.3		1.2		-1.40	2 (ID2, 3)	1	1	2	3
8	*Celastrus orbiculatus*	Bud	2.0		2.1		1.52	2 (ID2, 4)	1	1	4	2
9	*Actinidia arguta*	Bud	2.0		0.1		-3.51	1 (ID4)	1	1	4	2
10	Fern	Leaf	1.7		0.7		-1.38	1 (ID2)	2	1	1	2
11	*Pueraria lobata*	Seed	1.6		0		-4.76	1 (ID1)	1	2	3	-
12	*Actinidia arguta*	Bark	1.6		7.5	4	4.37	3 (ID2, 3, 4)	2	1	4	5
13	*Actinidia polygama*	Bud	1.5		0.4		-2.42	1 (ID4)	1	1	3	1
14	*Trifolium repens*	Root (Rhizome)	1.3		5.5	5	3.22	3 (ID1, 3, 4)	2	2	1	4
15	*Euonymus oxyphyllus*	Bark	1.1		1.2		-0.21	2 (ID2, 4)	2	1	3	4
16	*Evodiopanax innovans*	Bud	1.0		1.2		-1.67	1 (ID1)	1	1	3	2
17	*Pinus densiflora*	Seed (Pinecone)	0.7		10.4	2	5.10	4 (All)	1	2	5	-

18	*Hydrangea petiolaris*	Bud	0.7	1.9	1.08	2 (ID1, 3)	1	1	4	2
19	*Fraxinus lanuginosa*	Bark	0.7	2.6	2.31	2 (ID2, 4)	2	1	3	6
20	*Zanthoxylum ailanthoides*	Bark	0.7	1.5	3.21	1 (ID3)	2	1	4	3
21	*Euonymus oxyphyllus*	Bud	0.7	1.5	3.28	1 (ID4)	1	1	3	2
22	*Actinidia polygama*	Bark	0.7	1.5	3.83	1 (ID2)	2	1	3	5
23	*Celastrus orbiculatus*	Bark	0.2	1.4	2.84	1 (ID4)	2	1	4	6

※ Ranking in the time spent feeding for the top five underlined food items.

※※ Number of mother–infant pairs used in the calculation of the relative feeding index

※※※ “-” indicates that I did not measure the fracture toughness of the food item

TABLE II. Summary of the generalized linear mixed models for the effect of physical properties on the relative feeding index.

Adopted factor	AIC	ΔAIC	Akaike weight (%)
(a) 52 relative feeding indices involving 23 different food items			
Size +, Height +, Processing +	249.5	0	72
Size +, Height +	251.4	1.88	28
(b) 39 relative feeding indices involving 19 different food items, including toughness as the independent variable			
Size +, Height +, Processing +	185.3	0	59
Size +, Height +, Processing + , Toughness +	187.3	1.97	22

△*AIC* is the difference with the smallest Akaike information criterion (AIC). Akaike weight: exp(-0.5 × △AIC)/Σexp(0.5 × △AIC) [Burnham & Anderson, 2002].

"—" denotes a negative correlation between the relative feeding index and the physical property, while "+" denotes a positive correlation between them. A positive number for the relative feeding index indicates that infants fed less than their mothers did on a food item.

TABLE III. Best-fit generalized linear mixed model for the effect of physical properties on the relative feeding index.

Adopted factors	Partial regression coefficient	SE	Statistical test	Test statistic	*P*
(a) 52 relative feeding indices involving 23 different food items					
Size	3.25	0.71	Mann-Whitney test (N_1 = 27; N_2 = 25)	z =2.04	< 0.05
Processing	1.58	0.79	Mann-Whitney test (N_1 = 40; N_2 = 12)	z = 1.67	0.09
Height	1.57	0.26	Kruskal-Wallis test (N_1 = 19; N_2 = 6; N_3 = 13; N_4 = 10; N_5 = 4)	χ^2 = 16.7 d.f. = 4	< 0.01
(b) 39 relative feeding indices involving 19 different food items, including toughness as the independent variable					
Size	3.21	0.77	Mann-Whitney test (N_1 = 18; N_2 = 21)	z = 2.62	< 0.01
Processing	3.78	1.47	Mann-Whitney test (N_1 = 36; N_2 = 3)	z = 1.42	0.15
Height	1.38	0.35	Kruskal-Wallis test (N_1 = 11; N_2 = 6; N_3 = 12; N_4 = 10)	χ^2 = 9.2 d.f. = 3	< 0.05

The coefficient is from maximum-likelihood estimation. SE is the standard error of the coefficient.

Figure Legends

Fig. 1. Relationship between the relative feeding index and physical properties.

A negative number indicates that infants fed more than their mothers did on a food item, while a positive number indicates that infants fed less than their mothers did on a food item. The means of each food item in Table I are plotted. The number on the right side of the plot represents the food item number in Table I.

(a) Size: Food item size was classified into 2 categories: (1) small: eaten by infants in 1 bite, and (2) large: eaten by infants in two or more bites.

(b) Processing: The need for processing food items was divided into 2 categories: (1) no processing required before a food item was taken into the mouth, and (2) processing required before a food item was taken into the mouth.

(c) Height: The average height of food items where feeding was observed was classified into 5 categories: (1) 0 m (i.e., on the ground), (2) 0–2 m, (3) 2–5 m, (4) 5–10 m, and (5) more than 10 m.

(d) Fracture Toughness: The average fracture toughness of the food items was classified into 6 categories: (1) less than 500 J/m^2, (2) 500–1000 J/m^2, (3) 1000–1500 J/m^2, (4) 1500–2000 J/m^2, (5) 2000–2500 J/m^2, and (6) more than 2500 J/m^2

Fig. 2. Relationship between fracture toughness and the percentage of time spent feeding.

The fracture toughness of 32 food items that the macaques were observed to use their incisors to make the initial bites was measured.

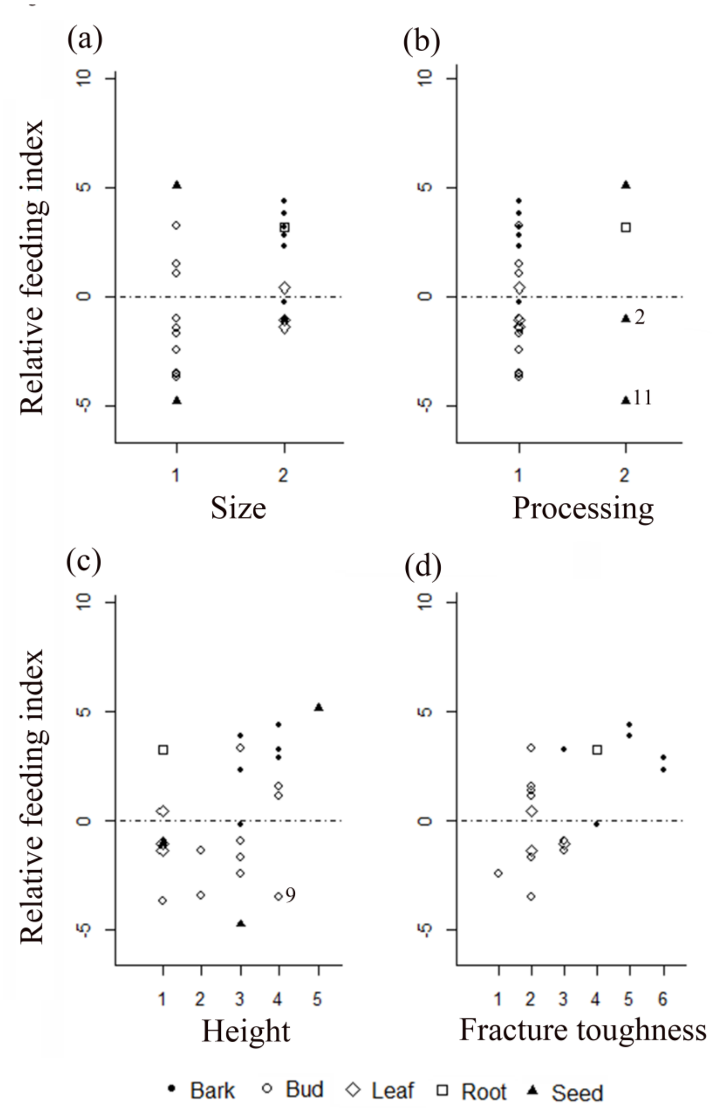

Fig. 1. Relationship between the relative feeding index and physical properties.

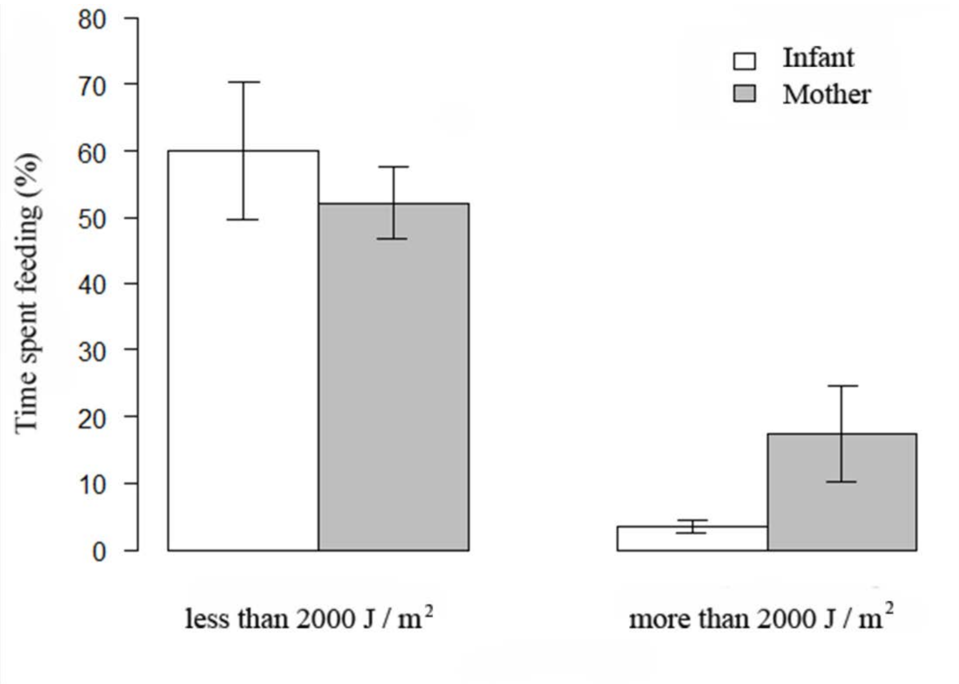

Fig.2. Relationship between fracture toughness and the percentage of time spent feeding.